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## DETERMINATION OF WILTING

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 241

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(WITH FIVE FIGURES)

The status of the question of permanent wilting in plants, as described by BRIGGS and SHANTZ (5, 6, 7, 8), CALDWELL (11), SHIVE and LIVINGSTON (37), and ALWAY (1), centers about the determination made by BRIGGS and SHANTZ that a plant is regarded as having attained a condition of permanent wilting when it does not recover its turgidity in a period of 24 hours when surrounded by air saturated with water vapor. The method of employing standardized hygrometric paper (2, 3, 4, 28, 30, 38, 40, 42) in the measurement of the transpiring power in plants consists in ascertaining the power of a leaf to give off water and comparing this with the power represented by a saturated blotting paper surface at the same time. This is then a measure in both cases of the resistance to the passage of water. The conditions which affect such measurements are internal, but these internal factors are dependent upon external factors. It is obvious, therefore, that data derived will be more or less of a resultant complex of all the forces which have been operative during the history of the plant.

The method in principle is the same as has previously been used in investigations upon the foliar transpiring power of plants. In the present studies filter paper circles (Munktell's Swedish

no. 00—11 cm.)[1] are impregnated with 3 per cent solution of cobalt chloride and are later cut into small squares. Just before using, these squares are heated over a bicycle lamp, or on a granite pie-plate suspended by a clamp over the flame of an alcohol lamp, until they become blue. One of these squares is placed between the jaws of a "transpiration clip," and as quickly as possible applied to either the upper or lower surface of a leaf. The time required to change the paper square from blue to pink is determined in seconds. The time which it takes to change a similar piece of cobalt paper from blue to pink when placed over a moist blotting paper surface blanketed by a millimeter of air (**2, 4, 28, 30, 34, 42**) is recorded. The water apparatus is the same as used by BAKKE and LIVINGSTON (**4**). TRELEASE and LIVINGSTON (**42**) have developed the relations of the temperature to vapor tension as first shown by BAKKE (**2**). These authors have presented a formula whereby the time interval may be ascertained on knowing the temperature. LIVINGSTON and SHREVE (**30**) have recently improved and modified this method. The principal improvement is in the adoption of permanent color standards. Instead of the simple square of cobalt chloride paper, a composite slip is employed consisting of a small piece of the hygrometric paper in juxtaposition with two slips having permanent color standards. These provide both an initial and an end point for the color change. For use in the laboratory they advocate and describe a simpler form of standard water evaporating apparatus. These modifications were not used in this study.

The possibilities of using the original method of standardized hygrometric paper in determining the extent of wilting and the permanent wilting point was first suggested to me by its author, B. E. LIVINGSTON, at the Desert Laboratory of the Carnegie Institution during the summer of 1913. In 1914 the writer (**3**), working at the Desert Laboratory, performed a series of measurements upon sunflower plants lifted from the soil and later brought into the laboratory to wilt. The results of this series of tests show that

[1] LIVINGSTON and SHREVE in a more recent publication (Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. Plant World **19**: 287–309. 1916) have recommended Whatman's filter no. 30 (11 cms.) circles as being superior to the Swedish paper.

wilting occurs at a definite point and that permanent wilting represents the most intense wilting possible, without serious rupture of the water columns of the plant. These studies have been amplified in the present investigation. The experimentation involved in the present study was performed in the greenhouse of the University of Chicago during the summers of 1915 and 1916. The large Russian variety of the common sunflower (*Helianthus annuus*) was used, the seed being from W. W. BARNARD of Chicago. The experiments involving the porometer were performed in the laboratory of Plant Physiology of Iowa State College. The plants were the same variety, but seed was secured from the Iowa Seed Company of Des Moines, Iowa.

## Series of 1915

### METHOD

The seeds used in the tests for 1915 were planted in sheet iron containers 6×6 inches, on June 31. Germination was forced by placing the containers in a warm house. When the cotyledons had made their appearance, the seedlings were thinned out so that only 3 remained. The cultures were then removed to a cooler place, where the plants were allowed to grow until they were approximately 6 weeks old and about 40 cm. high. The soil used in this series consisted of 4 parts of compost and 1 part sand. The water-holding capacity was calculated to be 47 per cent. The plants remained in the same containers throughout the entire period of the experiment. They were watered from time to time until the morning of July 13, when they were heavily watered, and after that no more water was added until the morning of July 16, when the plants were lightly watered and the soil surface covered with plasticine. Two plants were used as checks in testing out wilting by the BRIGGS and SHANTZ method.

The values for the indices of foliar transpiring power were obtained according to the original Livingston method; the standard water apparatus was the same as described by BAKKE and LIVINGSTON. Throughout the series, cobalt paper squares made from Munktell's Swedish no. 00 filter paper were used. As the work was carried on in the greenhouse, the usual bicycle lamp

for lighting was replaced by electric light. The cobalt paper squares were warmed upon a granite pie-plate, which was adjusted by a clamp over an alcohol flame, so that the paper squares were heated to a temperature sufficient to give them the blue color.

## EXPERIMENTATION

The readings for the 1915 series, begun on August 16, were usually made between the 10th and 11th hours and again between the 20th and 21st hours. Two plants were used for the foliar transpiring power tests; two additional plants were used for the wilting determinations according to the method of BRIGGS and SHANTZ. Evaporation was determined at the same time by a standardized Livingston form of cylindrical atmometer. The readings as recorded in table I show the maximum foliar transpiring power as occurring about the 11th hour, while the minimum usually occurs after sunset. Wherever possible, leaves of different ages were used and were numbered and tagged $\mathrm{I}a_1$, $\mathrm{I}a_2$, $\mathrm{I}a_3$, $\mathrm{I}b_1$, $\mathrm{I}b_2$, etc., the highest number representing the youngest leaf. In this way the same leaf could be used throughout.

The average results of the foliar transpiring power indices, as represented graphically (fig. 1), show a general decline from August 16 to August 20. The maximum index reached on August 17 possesses a value of 0.89. This index is almost the same as the one obtained earlier by BAKKE and LIVINGSTON. Although the plants were watered a little on the day the experiment was begun, they must have given off considerable water during the previous 3-day interval. That the soil moisture content has an appreciable effect upon foliar transpiring power has been proven previously, and from the nature of transpiration it is self-evident. The *Helianthus* plants of BAKKE and LIVINGSTON were growing in a place where the soil moisture was less than would be regarded as optimum. In all probability the two sets of *Helianthus* plants were grown in soil having practically the same amount of moisture. The soil moisture content in both series was below the amount necessary for the production of the greatest growth.

For the first half of the series the highest transpiring power occurs during the day, while the lowest transpiring power values

are at night. The average day values are accordingly 0.72, 0.92, 0.74, 0.38, 0.26, 0.19, 0.32 for one set (I*a*); for the other (I*b*), 0.61, 0.89, 0.76, 0.30, 0.30, 0.39, 0.42. The average night values for the first series are 0.29, 0.34, 0.24, 0.19, 0.25, 0.44, 0.69; for the second series, 0.31, 0.39, 0.23, 0.16, 0.50, 0.45, 0.61. The results obtained by calculating the ratio of the respective day and night values are rather uniform. For August 16 the average ratio is 2.4; for August 17, 2.7; the remaining values for I*a* are 3.1, 2.0, 1.0, 0.43, 0.46. The corresponding respective values for series I*b* are 2.0, 2.3, 3.3, 1.9, 0.77, 0.87, 0.61. For the first two days, August 16 and 17, the probable normal ratio is between 2 and 3. On the following day there is a slight increase, and after that there is a decrease. Whether the rise in the ratio on the third day presents a normal situation or not cannot at present be stated; at any rate the value is not far from 3. The decrease in foliar transpiring power after August 19 and the resulting decrease in the ratio do not show any definite mathematical relation. For a plant growing in a normal environment, a rise in evaporation will give an increase in transpiring power, but on August 22 there is a high evaporation, a low foliar transpiring power, and a lower day value than night value. Such a status must be looked upon as abnormal for growing plants. Beginning with August 21 there is a rapid ascent.

Considerable agreement is present between the graphs in this series and the one for *Helianthus* (**3**), where the plants were lifted from the soil. There is a decrease in the foliar transpiring power to a point where there is more or less of a balance, and then again where there is an increase. The time element in the present series is extended over a longer period, and as a result variations which might be masked in the series of short duration would be present.

The rupture of the water columns of the plants of the 1915 series is as definite as that presented for the plants lifted from the soil in southern Arizona. The outstanding feature of the curve is the very marked rise on August 20. Upon examination of the rate of evaporation, it will be at once evident that the evaporating power of the air was very low throughout. Two plants of this

## TABLE I

INDICES OF FOLIAR TRANSPIRING POWER FOR 3 DIFFERENT LEAVES OF TWO *Helianthus* PLANTS DURING PROGRESSIVE MARCH OF WILTING FROM AUGUST 16–22, 1915 (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

| LEAF NUMBER | DAY AND HOUR OF OBSERVATION | INDEX OF TRANSPIRING POWER | | | EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR | DAY AND HOUR OF OBSERVATION | INDEX OF TRANSPIRING POWER | | | EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR | RELATION OF DAY TO NIGHT |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Lower | Upper | Entire | | | Lower | Upper | Entire | | |
| $Ia_1$ | August 16 11:00 | 0.64 | 0.49 | 0.56 | .......... | August 16 20:00 | 0.27 | 0.18 | 0.23 | 0.45 | 2.4 |
| $Ia_2$ | | 0.94 | 0.52 | 0.73 | | | 0.36 | 0.23 | 0.30 | | 2.4 |
| $Ia_3$ | | 0.98 | 0.74 | 0.86 | | | 0.41 | 0.27 | 0.34 | | 2.5 |
| | | Average 0.85 | 0.58 | 0.72 | | | 0.35 | 0.23 | 0.29 | | 2.4 |
| $Ib_1$ | 11:00 | 0.74 | 0.36 | 0.55 | | | 0.41 | 0.19 | 0.30 | | 1.8 |
| $Ib_2$ | | 0.94 | 0.39 | 0.67 | | | 0.40 | 0.22 | 0.31 | | 2.2 |
| | | Average 0.84 | 0.38 | 0.61 | | | 0.41 | 0.21 | 0.31 | | 2.0 |
| $Ia_1$ | August 17 10:00 | 0.89 | 0.80 | 0.85 | 0.40 | August 17 21:00 | 0.39 | 0.20 | 0.30 | 0.17 | 2.8 |
| $Ia_2$ | | 0.94 | 0.94 | 0.94 | | | 0.42 | 0.24 | 0.33 | | 2.8 |
| $Ia_3$ | | 0.97 | 0.97 | 0.97 | | | 0.48 | 0.32 | 0.40 | | 2.4 |
| | | Average **0.93** | **0.90** | **0.92** | | | 0.43 | 0.25 | 0.34 | | 2.7 |
| $Ib_1$ | | 0.97 | 0.64 | 0.80 | | | 0.52 | 0.24 | 0.38 | | 2.1 |
| $Ib_2$ | | 0.97 | 0.97 | 0.97 | | | 0.51 | 0.29 | 0.40 | | 2.4 |
| | | Average **0.97** | **0.81** | **0.89** | | | 0.52 | 0.27 | 0.39 | | 2.3 |
| $Ia_1$ | August 18 | 0.74 | 0.16 | 0.45 | 0.18 | August 18 20:00 | 0.29 | 0.14 | 0.22 | 0.64 | 2.0 |
| $Ia_2$ | | 0.84 | 0.84 | 0.84 | | | 0.32 | 0.17 | 0.24 | | 3.5 |
| $Ia_3$ | | 0.97 | 0.89 | 0.93 | | | 0.34 | 0.16 | 0.25 | | 3.7 |
| | | Average 0.85 | 0.63 | 0.74 | | | 0.32 | *0.15* | 0.24 | | 3.1 |
| $Ib_1$ | | 0.67 | 0.62 | 0.65 | | | 0.32 | 0.18 | 0.25 | | 2.6 |
| $Ib_2$ | | 0.91 | 0.82 | 0.86 | | | 0.26 | 0.17 | 0.21 | | 4.1 |
| | | Average 0.79 | 0.72 | 0.76 | | | 0.29 | 0.18 | 0.23 | | 3.3 |
| $Ia_1$ | August 19 10:00 | 0.51 | 0.35 | 0.43 | 0.06 | August 19 20:00 | 0.21 | 0.16 | 0.18 | 0.67 | 2.4 |
| $Ia_2$ | | 0.38 | 0.32 | 0.35 | | | 0.24 | 0.21 | 0.22 | | 1.6 |
| $Ia_3$ | | 0.40 | 0.35 | 0.37 | | | 0.21 | 0.13 | 0.17 | | 2.1 |
| | | Average 0.43 | 0.34 | 0.38 | | | *0.22* | 0.17 | *0.19* | | 2.0 |
| $Ib_1$ | | 0.37 | 0.22 | 0.30 | | | 0.20 | 0.13 | 0.17 | | 1.8 |
| $Ib_2$ | | 0.37 | 0.23 | 0.30 | | | 0.18 | 0.13 | 0.15 | | 2.0 |
| | | Average 0.37 | *0.23* | *0.30* | | | *0.19* | *0.13* | *0.16* | | 1.9 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $Ia_1$ | August 20 11:00 | 0.31 | 0.18 | 0.24 | 0.08 | August 20 21:00 | 0.27 | 0.27 | 0.27 | 0.27 | 0.89* |
| $Ia_2$ | | 0.30 | 0.21 | 0.26 | | | 0.27 | 0.19 | 0.23 | | 1.10 |
| $Ia_3$ | | 0.31 | 0.24 | 0.27 | | | 0.25 | 0.24 | 0.25 | | 1.10 |
| | | Average 0.30 | 0.21 | 0.26 | | | 0.26 | 0.23 | 0.25 | | 1.00 |
| $Ib_1$ | | 0.33 | 0.24 | 0.28 | | | 0.38 | 0.32 | 0.35 | | 0.80 |
| $Ib_2$ | | 0.30 | 0.33 | 0.32 | | | 0.44 | 0.41 | 0.43 | | 0.75 |
| | | Average *0.32* | 0.29 | *0.30* | | | 0.75 | 0.69 | 0.72 | | 0.77* |
| | | | | | | | 0.52 | 0.47 | 0.50 | | 0.91 |
| $Ia_1$ | August 21 11:00 | 0.20 | 0.15 | 0.18 | 0.06 | August 21 21:00 | 0.83 | 0.29 | 0.56 | 0.24 | 0.34 |
| $Ia_2$ | | 0.26 | 0.17 | 0.22 | | | 0.60 | 0.37 | 0.49 | | 0.45 |
| $Ia_3$ | | 0.23 | 0.12 | 0.18 | | | 0.28 | 0.24 | 0.26 | | 0.69 |
| | | Average *0.23* | *0.15* | *0.19* | | | 0.57 | 0.33 | 0.44 | | 0.43 |
| $Ib_1$ | | 0.39 | 0.17 | 0.28 | | | 0.78 | 0.43 | 0.61 | | 0.46 |
| $Ib_2$ | | 0.31 | 0.17 | 0.24 | | | 0.59 | 0.42 | 0.51 | | 0.47 |
| $Ib_3$ | | 0.67 | 0.62 | 0.64 | | | 0.27 | 0.27 | 0.27 | | 2.30 |
| | | Average 0.46 | 0.32 | 0.39 | | | 0.54 | 0.37 | 0.46 | | 0.87 |
| $Ia_1$ | August 22 11:00 | 0.69 | 0.29 | 0.49 | 0.04 | August 22 21:00 | 0.70 | 0.60 | 0.65 | 0.66 | 0.75 |
| $Ia_2$ | | 0.34 | 0.21 | 0.27 | | | 0.73 | 0.73 | 0.73 | | 0.37 |
| $Ia_3$ | | 0.24 | 0.15 | 0.19 | | | 0.73 | 0.63 | 0.68 | | 0.30 |
| | | Average 0.42 | 0.22 | 0.32 | | | **0.72** | **0.65** | **0.69** | | 0.46 |
| $Ib_1$ | | 0.62 | 0.50 | 0.56 | | | 0.80 | 0.83 | 0.82 | | 0.68 |
| $Ib_2$ | | 0.48 | 0.29 | 0.38 | | | 0.85 | 0.82 | 0.83 | | 0.46 |
| $Ib_3$ | | 0.34 | 0.28 | 0.31 | | | 0.43 | 0.42 | 0.42 | | 0.74 |
| | | Average 0.48 | 0.36 | 0.42 | | | **0.69** | **0.69** | **0.69** | | 0.61 |

* Since the experiment has been in progress a new leaf has become of sufficient size so that it was large enough for the application of the clip. For August 21 then the index 0.72 is much higher than any of the others. This will naturally increase the average. In computing the average for the index, this last number was not used; 0.77 is the average for leaves $Ib_1$ and $Ib_2$.

same series were used for the determination of wilting according to the method of BRIGGS and SHANTZ. The results are given

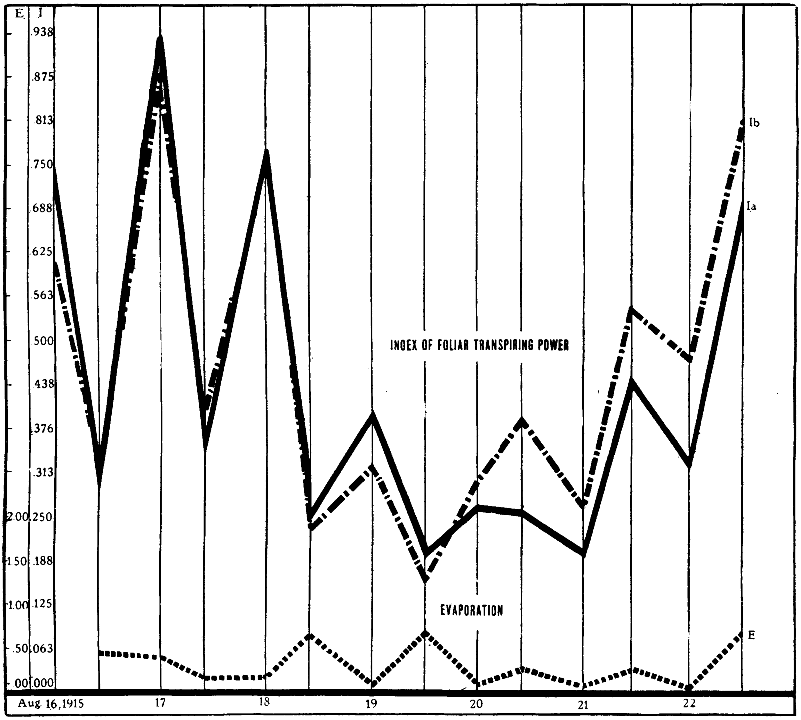


FIG. 1

in table II; those obtained giving the residual moisture at the time of wilting agree rather closely for the determinations made according to the two methods. In the method of BRIGGS and

TABLE II

| Method | 1 | 2 | Average |
|---|---|---|---|
| Briggs and Shantz......... | 10.38 | 7.84 | 9.11 |
| Hygrometric paper......... | 8.20 | 8.34 | 8.27 |

SHANTZ there is a greater variation than is found to be present where the hygrometric paper is used.

The breaking point occurring on August 21 is not far from the normal minimum value of the daily march of foliar transpiring power. From previous work upon the march of foliar transpiring power, there is more or less of a definite maximum (usually during the day) as well as a definite minimum (usually during the night). It seems that, in all probability, the minimum in the foliar transpiring power indicates approximately the greatest resistance to transpirational water loss. If the water content of the soil coupled with the evaporating power of the air is of such magnitude as to increase the resistance to the passage of water, so that the day maximum has a value as low or lower than the diurnal minimum (at night), the plant is then in a critical condition; at least this has been found to be true for *Helianthus*. For the entire leaf surface the transpiring power ratios at night are as follows: (1) I*a*, −0.23, 0.30, 0.34; (2) I*b*, −0.30, 0.31. On August 20 the respective values are 0.24, 0.26, 0.27 for I$a_2$, and 0.28 and 0.32 for I$b_2$. The average ratio for the first is 2.2 and the average ratio for the test on August 20 is 0.91. On August 21 the ratio is less; on the following day it is a little higher.

The entire situation as here brought forward centers about the amount of moisture present in the soil during the march of wilting when the index of transpiring power ratio of day to night comes to be represented by unity or less. The duration of this ratio may be an important factor in obtaining data that will give information on the relative drought resistance of plants.

## Series of 1916

### METHOD

The method of procedure in the experimentation for 1916 was much the same as for the previous season. The sheet iron containers were a little deeper (7 inches instead of 6). The soil mixture was lighter than before, containing 1 part of clean pure sand mixed with 3 parts of rich garden soil, and the variety the same as before (Mammoth Russian). The seeds were planted on June 24, and on July 1 the seedlings were 5 cm. high and were then transplanted. Three plants were set deeply in the soil. The cultures

were then placed in the greenhouse and were watered from time to time. A Livingston standard atmometer of the cylindrical form was set up in close proximity to measure evaporation. Readings were taken of the atmometer whenever a reading was made of the transpiring power. On July 19 the plants were thoroughly watered and were lightly watered again on July 20. On July 21 the containers were sealed over with plasticine preparatory to making hourly readings of the foliar transpiring power for a period of twenty-four consecutive hours. For the measurements upon the index of foliar transpiring power the same apparatus as employed before was used. On the 18th hour of July 22 the last reading was made for the daily march of foliar transpiring power. Beginning July 24, readings were taken three times during the day: (1) at approximately 10:00 A.M., (2) at the 14th or 15th hour, and (3) at some time during the night. The times chosen really represent the three important periods during the daily march, for the first one gives this value at a time when the transpiring power is near its maximum, the second when evaporation is at its maximum, and the third when the index of transpiring power has its lowest value. The leaves were tagged as before so that the same leaves were used throughout.

The soil surface of several additional plants was coated over with plasticine to serve as a comparison or check for the plants used for the determination of foliar transpiring power. In applying the cobalt paper squares from day to day, it became easy to judge the condition of the plant. When plants presenting a physical state such as was in evidence for leaf I$a_2$ on August 3, and for leaf I$b_2$ on August 7, were placed in a moist chamber, they failed to recover. It was then deemed unnecessary to test further. At the time of the beginning of the experiment plant I*a* was 25 cm. high, while plant I*b* was 28 cm. high.

## INDICES OF FOLIAR TRANSPIRING POWER

In using the method of standardized hygrometric paper for the determination of the indices of foliar transpiring power, two separate plants were used. The method of numbering the leaves was the same as for the 1915 series. From plant I*a* two leaves

were chosen, $Ia_1$ having the dimensions $5 \times 8$ cm., and $Ia_2$, $4 \times 6$ cm.; from plants $Ib$ two leaves were chosen, $Ib_1$, $7 \times 9$ cm., and $Ib_2$, $3 \times 4$ cm. Whenever a new leaf became sufficiently large for the application of the clip, approximately $3 \times 4$ cm., it was included with the others. The readings were begun on the 18th hour of July 21 and continued at hourly intervals for 24 hours. Readings were taken at the same time from a standardized Livingston cylindrical form of atmometer. The results for plant $Ia$ are given in table III.

This series shows that the march of the foliar transpiring power is the same as has previously been pointed out (**2, 4, 28, 40**), in that the maximum transpiring power is attained at a time previous to the greatest evaporation. The highest index occurs usually at the 10th and 11th hours, while the evaporation maximum occurs usually on the 14th hour. On account of the larger number of readings it is to be expected that the graphical representation (fig. 2) will show less abruptness than has formerly been presented.

Recalling that the leaf represented by $Ia_1$ is older than $Ia_2$, it is plain that the index of foliar transpiring power is higher for the younger leaf almost entirely throughout the 24-hour period. The maximum for $Ia_1$ is at the 11th hour, when it is 0.93. This value is again in evidence 2 hours later. For $Ia_2$ the highest value is at the 10th hour, when the transpiring power value is 1.00. This same value is again reached at the 12th hour. It is evident that the younger leaf $Ia_2$ reaches its maximum at an earlier period than the older leaf $Ia_1$. This feature substantiates similar conclusions reached by BAKKE and LIVINGSTON. Another important feature in connection with the graph showing the march of foliar transpiring power is the sudden drop for both leaves. The lowest point (0.59 for $Ia_1$ and 0.67 for $Ia_2$) occurs on the 14th hour. At the 15th hour the index values are respectively 0.91 and 0.93, while the corresponding values at the 13th hour are 0.93 and 0.83. Although the drop is the feature in the afternoon readings, the recovery occurring at the 15th hour is always below that of the forenoon maximum. In the present case there is not much difference, being 0.91 for $Ia_1$; for the younger leaves there is a greater variation, being 0.93 at 15:00 o'clock and 1.00 for the 10:00 and 13:00 o'clock readings. At the 14th hour the average reading for the

TABLE III

DATA FOR MARCH OF INDICES OF FOLIAR TRANSPIRING POWER FOR *Helianthus* PLANT I*a* (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

| LEAF NUMBER | TIME OF OBSERVATION | TIME OF COLOR CHANGE IN SECONDS | | INDEX OF TRANSPIRING POWER | | | EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR |
|---|---|---|---|---|---|---|---|
| | | Lower surface | Upper surface | Lower surface | Upper surface | Entire leaf | |
| | July 21 | | | | | | |
| I$a_1$....... | 18:15 | 31 | 52 | 0.77 | 0.46 | 0.62 | |
| I$a_2$....... | 18:20 | 24 | 46 | **1.00** | 0.52 | 0.76 | |
| I$a_1$....... | 19:10 | 42 | 65 | 0.68 | 0.44 | 0.56 | 0.22 |
| I$a_2$....... | 19:15 | 38 | 55 | 0.75 | 0.52 | 0.64 | |
| I$a_1$....... | 20:15 | 46 | 59 | 0.62 | 0.49 | 0.56 | 0.15 |
| I$a_2$....... | 20:20 | 40 | 54 | 0.73 | 0.54 | 0.64 | |
| I$a_1$....... | 21:10 | 45 | 72 | 0.64 | 0.40 | 0.52 | 0.16 |
| I$a_2$....... | 21:10 | 40 | 50 | 0.73 | 0.58 | 0.66 | |
| I$a_1$....... | 22:10 | 51 | 77 | 0.61 | 0.40 | 0.51 | *0.09* |
| I$a_2$....... | 22:15 | 40 | 65 | 0.78 | 0.48 | 0.63 | |
| I$a_1$....... | 23:10 | 56 | 74 | *0.57* | 0.43 | *0.50* | 0.15 |
| I$a_2$....... | 23:10 | 45 | 69 | 0.71 | 0.46 | 0.59 | |
| | July 22 | | | | | | |
| I$a_1$....... | 24:10 | 50 | 90 | 0.66 | *0.37* | 0.52 | 0.18 |
| I$a_2$....... | 24:15 | 42 | 77 | 0.79 | 0.43 | 0.62 | |
| I$a_1$....... | 1:10 | 48 | 88 | 0.71 | 0.38 | 0.55 | 0.12 |
| I$a_2$....... | 1:15 | 42 | 74 | 0.81 | 0.46 | 0.64 | |
| I$a_1$....... | 2:10 | 57 | 90 | 0.63 | 0.40 | 0.52 | 0.15 |
| I$a_2$....... | 2:15 | 49 | 85 | 0.74 | *0.42* | *0.58* | |
| I$a_1$....... | 3:10 | 55 | 85 | 0.65 | 0.42 | 0.54 | 0.15 |
| I$a_2$....... | 3:15 | 50 | 75 | 0.72 | 0.48 | 0.60 | |
| I$a_1$....... | 4:10 | 50 | 85 | 0.72 | 0.42 | 0.57 | 0.15 |
| I$a_2$....... | 4:15 | 46 | 78 | 0.78 | 0.46 | 0.62 | |
| I$a_1$....... | 5:10 | 50 | 62 | 0.72 | 0.58 | 0.65 | 0.15 |
| I$a_2$....... | 5:15 | 45 | 57 | 0.80 | 0.63 | 0.72 | |
| I$a_1$....... | 6:10 | 39 | 50 | 0.87 | 0.68 | 0.78 | 0.15 |
| I$a_2$....... | 6:15 | 36 | 50 | 0.94 | 0.68 | 0.81 | |
| I$a_1$....... | 7:10 | 36 | 42 | 0.81 | 0.69 | 0.75 | 0.15 |
| I$a_2$....... | 1:10 | 36 | 37 | 0.81 | 0.78 | 0.80 | |
| I$a_1$....... | 8:15 | 30 | 42 | 0.77 | 0.55 | 0.66 | 0.15 |
| I$a_2$....... | 8:20 | 28 | 32 | 0.82 | 0.72 | 0.77 | |
| I$a_1$....... | 9:05 | 24 | 24 | 0.88 | 0.88 | 0.88 | 0.22 |
| I$a_2$....... | 9:05 | 22 | 22 | 0.95 | 0.95 | 0.95 | |
| I$a_1$....... | 10:05 | 22 | 24 | **0.95** | 0.88 | 0.92 | 0.58 |
| I$a_2$....... | 10:05 | 21 | 21 | **1.00** | *1.00* | **1.00** | |
| I$a_1$....... | 11:00 | 21 | 20 | 0.91 | **0.95** | 0.93 | .......... |
| I$a_2$....... | 11:00 | 20 | 20 | 0.95 | 0.95 | 0.95 | |
| I$a_1$....... | 12:00 | 21 | 21 | 0.86 | 0.86 | 0.86 | .......... |
| I$a_2$....... | 12:00 | 18 | 18 | *1.00* | *1.00* | **1.00** | |
| I$a_1$....... | 13:10 | 16 | 16 | 0.93 | 0.93 | 0.93 | 1.0 |
| I$a_2$....... | 13:10 | 18 | 18 | 0.83 | 0.83 | 0.83 | |
| I$a_1$....... | 14:10 | 17 | 17 | 0.59 | 0.59 | 0.59 | 1.2 |
| I$a_2$....... | 14:15 | 15 | 15 | 0.67 | 0.67 | 0.67 | |
| I$a_1$....... | 15:10 | 15 | 16 | 0.93 | 0.88 | 0.91 | 1.2 |
| I$a_2$....... | 15:15 | 15 | 15 | 0.93 | 0.93 | 0.93 | |
| I$a_1$....... | 16:15 | 17 | 18 | 0.88 | 0.88 | 0.88 | **1.6** |
| I$a_2$....... | 16:20 | 21 | 21 | 0.71 | 0.71 | 0.71 | |
| I$a_1$....... | 17:00 | 19 | 19 | **0.95** | **0.95** | **0.95** | 1.0 |
| I$a_2$....... | 17:00 | 18 | 20 | **1.00** | 0.90 | 0.95 | |
| I$a_1$....... | 18:00 | 25 | 35 | 0.80 | 0.57 | 0.69 | 1.0 |
| I$a_2$....... | 18:05 | 20 | 25 | **1.00** | 0.80 | 0.90 | |

older leaves ($Ia_1$) is 0.59 and for the younger leaves is 0.67. The differences then in the order given are 0.33 and 0.34. The respective values on the 15th hour are 0.91 and 0.93. These give recovery value differences of 0.32 and 0.26. The drop in the afternoon reading is not a new thing, either in foliar transpiring power or in transpiration. No doubt this great resistance to the

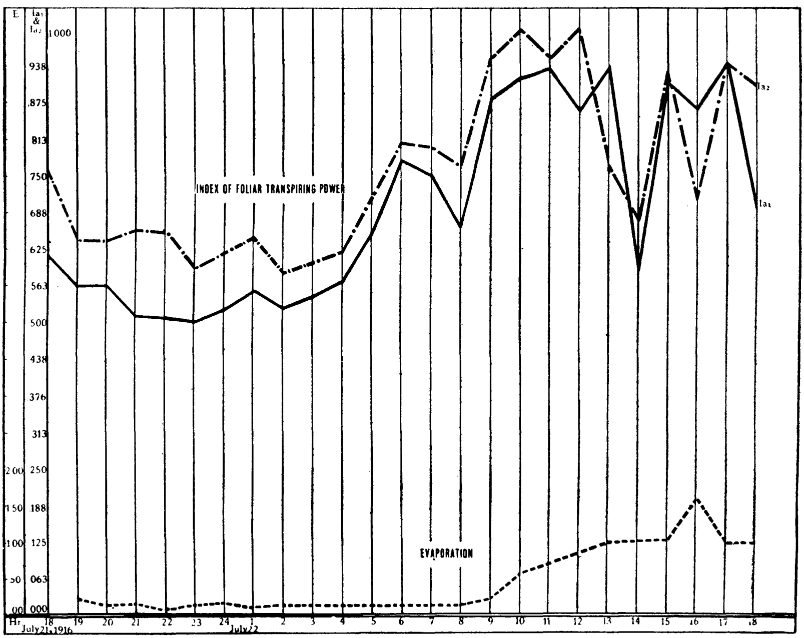


FIG. 2

passage of water is a condition of incipient drying. It may be that at this period, usually present at about the time of greatest evaporation, there is a lack of water, not only in the cells of the leaf, but also in the vessels themselves. SHREVE (40) has submitted evidence, at least theoretical, showing that variations in the transpiring power are due to variations in the water-holding capacity of the internal tissue. Using the DIXON (16, 17, 18) conception of continuous columns, as well as the results of the experiments of RENNER (34, 35, 36) upon transpiration, there is doubtless a greater tension present upon the water columns. If this is related to

absorption and incipient drying, an additional force must be present in order to cause the water to be pulled into the cells to a greater degree than before. If this interpretation is correct, the older leaves (on account of their closer proximity to the absorption center) should show a more complete revival. This speculation would necessarily be based upon the readings of the secondary maxima. The comparative values become evident, for I*a* has a maximum of 0.93, falls to 0.59, and subsequently returns to 0.91; for I$a_2$ the maximum is 1.00 and comes back from 0.97 to 0.86. This fall and subsequent rise are independent of the evaporation rate.

The march of the foliar transpiring power is more or less definite. This is especially true as it bears upon maximum and minimum values. For I*a* the maximum value occurs on the 11th hour with an index of 0.95, while the minimum value 0.50 is on the 23d hour. The ratio between maximum and minimum is 1.9. For I$a_2$ the maximum value, 1.00, is in evidence on the 10th hour, while the reading 0.58 on the 2d hour of July 22 gives the minimum value. The ratio in the latter case is 1.72.

Another important feature presented by the present series is the high value on the 17th hour of July 22. In the previous experiments which have dealt with foliar transpiring power, there has been a fall in the transpiring power value after the secondary rise. It is noticed that the evaporation during the afternoon is rather intense, being 1.6. The high value of the transpiring power, therefore, is without question due to the high evaporating power of the air.

In formulating a graph (fig. 3) from the data presented in the march of foliar transpiring power, the general feature is the high foliar transpiring power before the time of greatest diurnal evaporation. For both leaves the maximum is reached at the 11th hour, when the index is 1.00. This value is retained for I$b_1$ until the 12th hour, and for I$b_2$ until the 13th hour. The minimum value (0.47) for I$b_1$ occurs on the 22d hour, while for I$b_2$ (0.44) it occurs on the 18th hour. The ratio of maximum to minimum or of day value to night value is 2.1 for I$b_1$ and 2.3 for I$b_2$. The sudden drop in the afternoon reading on the 14th hour is equally as striking as that

# TABLE IV

DATA FOR MARCH OF INDICES OF FOLIAR TRANSPIRING POWER FOR *Helianthus* PLANT $Ib$ (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

| LEAF NUMBER | TIME OF OBSERVATION | TIME OF COLOR CHANGE IN SECONDS | | INDEX OF TRANSPIRING POWER | | | EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR |
|---|---|---|---|---|---|---|---|
| | | Lower surface | Upper surface | Lower surface | Upper surface | Entire leaf | |
| | July 21 | | | | | | |
| $Ib_1$....... | 18:25 | 27 | 63 | 0.89 | 0.38 | 0.64 | ........... |
| $Ib_2$....... | 18:25 | 44 | 73 | 0.55 | 0.33 | *0.44* | |
| $Ib_1$....... | 19:25 | 40 | 67 | 0.72 | 0.43 | 0.58 | 0.22 |
| $Ib_2$....... | 19:30 | 44 | 81 | 0.65 | 0.35 | 0.50 | |
| $Ib_1$....... | 20:25 | 41 | 68 | 0.71 | 0.43 | 0.57 | 0.15 |
| $Ib_2$....... | 20:25 | 43 | 78 | 0.67 | 0.37 | 0.52 | |
| $Ib_1$....... | 21:15 | 44 | 90 | 0.66 | *0.32* | 0.49 | 0.16 |
| $Ib_2$....... | 21:20 | 39 | 105 | 0.74 | *0.28* | 0.51 | |
| $Ib_1$....... | 22:20 | 52 | 95 | *0.60* | 0.33 | *0.47* | *0.09* |
| $Ib_2$....... | 22:25 | 50 | 97 | *0.62* | 0.32 | 0.47 | |
| $Ib_1$....... | 23:15 | 47 | 85 | 0.68 | 0.38 | 0.53 | 0.15 |
| $Ib_2$....... | 23:20 | 43 | 82 | 0.74 | 0.39 | 0.57 | |
| $Ib_1$....... | 24:20 | 53 | 78 | 0.62 | 0.42 | 0.52 | 0.18 |
| $Ib_2$....... | 24:20 | 49 | 73 | 0.67 | 0.45 | 0.56 | |
| | July 22 | | | | | | |
| $Ib_1$....... | 1:20 | 51 | 78 | 0.67 | 0.44 | 0.56 | 0.12 |
| $Ib_2$....... | 1:20 | 47 | 71 | 0.72 | 0.48 | 0.60 | |
| $Ib_1$....... | 2:20 | 57 | 75 | 0.63 | 0.48 | 0.56 | 0.15 |
| $Ib_2$....... | 2:20 | 50 | 72 | 0.72 | 0.50 | 0.61 | |
| $Ib_1$....... | 3:20 | 46 | 70 | 0.78 | 0.52 | 0.65 | 0.15 |
| $Ib_2$....... | 3:20 | 41 | 70 | 0.88 | 0.52 | 0.70 | |
| $Ib_1$....... | 4:20 | 49 | 90 | 0.73 | 0.40 | 0.57 | 0.15 |
| $Ib_2$....... | 4:20 | 43 | 75 | 0.84 | 0.48 | 0.66 | |
| $Ib_1$....... | 5:20 | 48 | 82 | 0.75 | 0.44 | 0.60 | 0.15 |
| $Ib_2$....... | 5:25 | 40 | 85 | 0.90 | 0.38 | 0.64 | |
| $Ib_1$....... | 6:20 | 42 | 50 | 0.81 | 0.68 | 0.75 | 0.15 |
| $Ib_2$....... | 6:20 | 46 | 55 | 0.74 | 0.62 | 0.68 | |
| $Ib_1$....... | 7:15 | 31 | 37 | 0.74 | 0.62 | 0.68 | 0.15 |
| $Ib_2$....... | 7:15 | 26 | 42 | 0.89 | 0.55 | 0.72 | |
| $Ib_1$....... | 8:25 | 25 | 31 | 0.92 | 0.74 | 0.84 | 0.15 |
| $Ib_2$....... | 8:25 | 25 | 28 | 0.92 | 0.82 | 0.87 | |
| $Ib_1$....... | 9:10 | 25 | 30 | 0.84 | 0.70 | 0.77 | 0.22 |
| $Ib_2$....... | 9:15 | 21 | 22 | 1.00 | 0.95 | 0.98 | |
| $Ib_1$....... | 10:10 | 25 | 26 | 0.84 | 0.81 | 0.83 | 0.58 |
| $Ib_2$....... | 10:10 | 23 | 24 | 0.91 | 0.88 | 0.90 | |
| $Ib_1$....... | 11:10 | 19 | 19 | **1.00** | **1.00** | **1.00** | ........... |
| $Ib_2$....... | 11:10 | 19 | 19 | **1.00** | **1.00** | **1.00** | |
| $Ib_1$....... | 12:10 | 18 | 18 | **1.00** | **1.00** | **1.00** | ........... |
| $Ib_2$....... | 12:10 | 18 | 18 | **1.00** | **1.00** | **1.00** | |
| $Ib_1$....... | 13:15 | 16 | 16 | 0.93 | 0.93 | 0.93 | 1.0 |
| $Ib_2$....... | 13:20 | 15 | 15 | **1.00** | **1.00** | **1.00** | |
| $Ib_1$....... | 14:15 | 14 | 15 | 0.71 | 0.67 | 0.69 | 1.2 |
| $Ib_2$....... | 14:20 | 17 | 17 | 0.59 | 0.59 | 0.59 | |
| $Ib_1$....... | 15:20 | 15 | 15 | 0.93 | 0.93 | 0.93 | 1.2 |
| $Ib_2$....... | 15:20 | 16 | 17 | 0.88 | 0.82 | 0.85 | |
| $Ib_1$....... | 16:25 | 16 | 18 | 0.94 | 0.83 | 0.89 | **1.6** |
| $Ib_2$....... | 16:25 | 17 | 19 | 0.88 | 0.79 | 0.84 | |
| $Ib_1$....... | 17:10 | 19 | 18 | 0.95 | 1.00 | 0.98 | 1.0 |
| $Ib_2$....... | 17:15 | 20 | 23 | 0.90 | 0.78 | 0.84 | |
| $Ib_1$....... | 18:10 | 27 | 30 | 0.74 | 0.67 | 0.71 | 1.0 |
| $Ib_2$....... | 18:15 | 30 | 33 | 0.67 | 0.61 | 0.64 | |

noted for series I*a*. For I$b_1$ the drop really begins on the 12th hour and falls from 1.00 to 0.69, giving a difference of 0.31; for I$b_2$ the fall is from 1.00 to 0.59, giving a difference of 0.41. The recovery for I$b_1$ is from 0.69 to 0.93, and for I$b_2$ is from 0.59 to 0.85. The difference value is 0.24 in one case and 0.26 in the other. It was pointed out for series I*a* that the recovery of the older leaf is more marked than that of the younger leaf. This

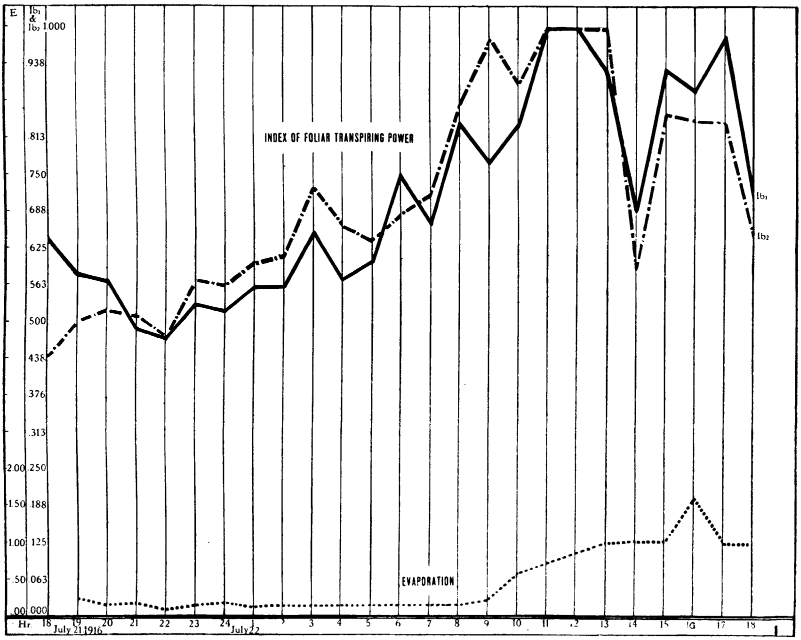


FIG. 3

feature is again borne out in the present series, where the values for I$b_1$ are in excess of those of I$b_2$.

For the reason that the leaves of series I$b_1$ are very nearly of the same age, the same variation as set forth in the previous season will not be in evidence. The minimum values are slightly lower. As a result the ratios between maxima and minima are respectively 2.19 and 2.27. The same high foliar transpiring power is present at the 17th hour. This agrees with the former series. The data submitted in table V give the march of foliar transpiring power during the process of wilting from July 24–August 7.

TABLE V

INDICES OF FOLIAR TRANSPIRING POWER DURING PROGRESS OF WILTING OF *Helianthus* PLANT Ia

| Time of observation | | Index of transpiring power entire leaf | | Evaporation from standardized atmometer, cc. per hour |
|---|---|---|---|---|
| | | $Ia_1$ | $Ia_2$ | |
| July 24 | 9:15........ | 0.51 | 0.68 | 1.00 |
| | 14:00........ | 0.53 | 0.54 | 1.23 |
| | 20:00........ | 0.28 | 0.39 | 0.73 |
| July 25 | 9:10........ | 0.49 | 0.29 | 0.24 |
| | 14:00........ | 0.27 | 0.23 | 0.71 |
| | 21:00........ | 0.59 | 0.31 | 0.66 |
| July 26 | 9:25........ | 0.51 | 0.31 | 0.11 |
| | 14:10........ | 0.70 | 0.20 | 0.91 |
| | 21:15........ | 0.49 | 0.21 | 0.62 |
| July 27 | 9:25........ | 0.43 | 0.20 | 0.02 |
| | 14:05........ | 0.65 | 0.18 | 1.25 |
| | 22:25........ | 0.69 | 0.18 | 0.51 |
| July 28 | 9:00........ | 0.38 | 0.16 | 0.12 |
| | 14:35........ | 0.22 | 0.14 | 1.12 |
| | 21:00........ | 0.36 | 0.19 | 0.66 |
| July 29 | 9:20........ | 0.33 | 0.18 | 0.13 |
| | 14:00........ | " | 0.15 | 0.80 |
| | 21:00........ | " | 0.13 | 0.69 |
| July 30 | 9:05........ | " | 0.21 | 0.28 |
| | 14:15........ | " | 0.12 | 0.18 |
| | 21:00........ | " | 0.16 | 0.91 |
| July 31 | 10:05........ | " | 0.34 | 0.26 |
| | 14:15........ | " | 0.17 | 1.11 |
| | 21:05........ | " | 0.09 | 0.66 |
| August 1 | 10:05........ | " | 0.17 | 0.24 |
| | 14:00........ | " | 0.15 | 0.71 |
| | 21:05........ | " | 0.13 | 0.41 |
| August 2 | 10:10........ | " | 0.14 | 0.24 |
| | 14:10........ | " | 0.15 | 1.09 |
| | 22:45........ | " | 0.16 | 0.53 |
| August 3 | 10:00........ | " | 0.14 | 0.34 |
| | 14:00........ | " | 0.12 | 1.50 |
| | 23:00........ | " | 0.16 | 0.37 |
| August 4 | 10:00........ | " | 0.17 | 0.22 |
| | 14:00........ | " | 0.12 | 1.03 |
| | 21:00........ | " | 0.17 | 1.18 |
| August 5 | 10:10........ | " | 0.17 | 0.33 |
| | 14:05........ | " | 1.17 | 0.77 |
| | 21:00........ | " | 0.11 | 0.21 |
| August 6 | 9:30........ | " | 0.14 | 0.11 |
| | 14:10........ | " | 0.11 | 1.49 |
| | 21:00........ | " | 0.13 | 1.10 |
| August 7 | 10:00........ | " | 0.13 | 0.49 |
| | 14:05........ | " | 0.23 | 0.74 |

From the tabulated data of table V, and from graph (fig. 4) of series I$a$, it is noticed that there is a marked decrease in foliar transpiring power from July 24 up to the time when the plant wilts. The transpiring power of leaf I$a_1$ is very irregular. There is no doubt but that the plant has attained its permanent wilting point on July 29, but because the leaves of this series are somewhat older than I$a_2$, and as they are located nearer the absorptive center their action will be more or less modified by the presence of the younger leaves at the tip. For the leaf I$a_2$ there is a marked decrease in the foliar transpiring power from July 24 to July 30, the foliar transpiring power being especially high on August 1. This feature is probably in response to the exceedingly high temperature at that time. The evaporation from the standardized atmometer bears out this statement. From August 1 to August 7 the index of foliar transpiring power proceeds almost in a straight line, except for small dips occurring in the majority of

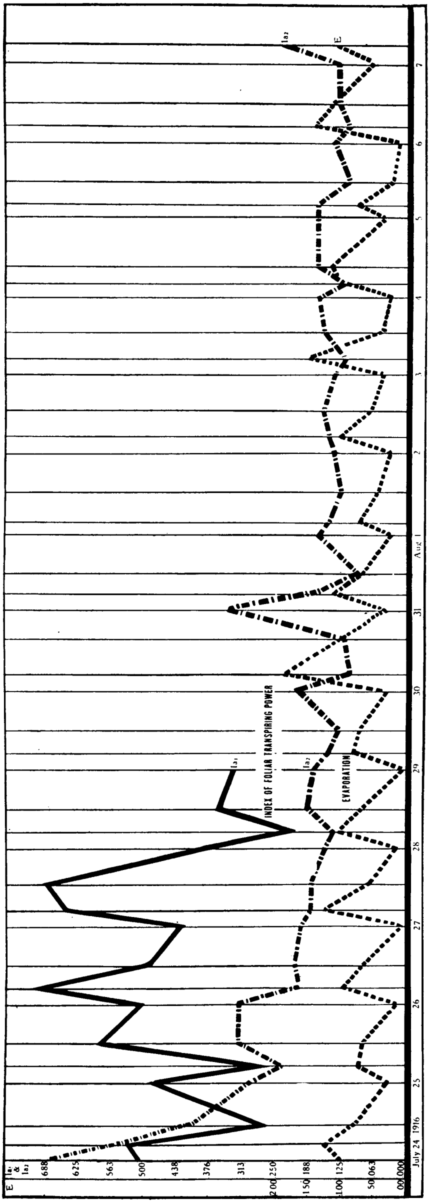


FIG. 4

cases when the evaporation was at its highest. This part of the graph conforms with the one obtained when the plants were lifted from the soil. On August 7 the index of foliar transpiring power increases from 0.13 to 0.23, or 77 per cent from the 10th hour to the 14th hour. On the previous day it dropped from 0.14 to 0.11, while on the preceding day the two indices were the same. At no other time during the march was there such a great percentage increase.

In obtaining the ratio between the day reading and the night reading for 24 consecutive hours, the day readings were usually made between the 9th and the 10th hours. For the night readings there was no need of selection as only one reading was taken. Beginning with July 24, and continuing until July 29 (time of wilting), the transpiring power indices representing the day readings for I$a_1$ are 0.51, 0.49, 0.51, 0.43, 0.38, 0.33, while the corresponding night values are 0.28, 0.59, 0.49, 0.69, 0.36, 0.33. The respective ratio values are 1.82, 0.83, 1.04, 0.62, 1.05. On July 21–22 the ratio between the reading on the 9th hour and the reading on the 21st hour is 0.88:0.52, or 1.7. For the entire 24-hour period the maximum and minimum ratio is 1.9. The only normal ratio is the first. It is interesting to note that for leaf I$a_1$ the minimum is normally 0.50. During the progress of wilting the maximum does not get below this point until July 27; after that it is below the usual minimum.

From July 24 to August 7 (time of wilting) the corresponding indices for I$a_2$ are present; for the morning 0.68, 0.29, 0.31, 0.20, 0.16, 0.18, 0.21, 0.34, 0.17, 0.14, 0.14, 0.17, 0.17, 0.14, 0.13; for the night 0.39, 0.31, 0.21, 0.18, 0.19, 0.13, 0.16, 0.09, 0.13, 0.16, 0.16, 0.17, 0.11, 0.13. The ratio of the day (morning) readings to the night readings is respectively 1.74, 0.94, 1.11, 0.84, 1.38, 1.31, 3.78, 1.31, 0.88, 0.88, 1.00, 1.54, 1.08. For July 21–22 the ratio of maximum to minimum for I$a_2$ is 1.72. For the corresponding hours the ratio is 0.95:0.66, or 1.44. On this basis, therefore, the readings of the first day are normal, in that the ratio is approximately the same as for the maximum to the minimum on July 21–22 (1.72). Also the maximum values during the march of wilting, with the exception of the first reading, are all

below the minimum set during the daily march of foliar transpiring power for July 21–22.

The data presented in table VI give results that harmonize with those of table V. As was stated in connection with the march of

TABLE VI

INDEX OF FOLIAR TRANSPIRING POWER DURING PROCESS OF WILTING OF *Helianthus* PLANT 1b.

| Time of observation | | Index of transpiring power entire leaf | | Evaporation from standardized atmometer, cc. per hour |
|---|---|---|---|---|
| | | $Ib_1$ | $Ib_2$ | |
| July 24 | 9:20 | 0.17 | 0.15 | 1.00 |
| | 14:00 | 0.18 | 0.21 | 1.23 |
| | 20:40 | 0.18 | 0.14 | 0.73 |
| July 25 | 9:00 | 0.12 | 0.20 | 0.24 |
| | 14:00 | 0.17 | 0.14 | 0.71 |
| | 21:10 | 0.19 | 0.21 | 0.66 |
| July 26 | 9:35 | 0.12 | 0.28 | 0.11 |
| | 14:15 | 0.18 | 0.12 | 0.91 |
| | 21:00 | 0.35 | 0.19 | 0.62 |
| July 27 | 9:30 | 0.10 | 0.13 | 0.02 |
| | 14:15 | 0.19 | 0.18 | 1.25 |
| | 22:00 | 0.34 | 0.20 | 0.51 |
| July 28 | 9:25 | 0.22 | 0.13 | 0.12 |
| | 14:45 | 0.19 | 0.14 | 1.12 |
| | 21:00 | 0.12 | 0.22 | 0.66 |
| July 29 | 9:30 | 0.25 | 0.16 | 0.13 |
| | 14:00 | 0.24 | 0.10 | 0.80 |
| | 21:00 | 0.14 | 0.11 | 0.69 |
| July 30 | 9:10 | 0.31 | 0.14 | 0.28 |
| | 14:20 | 0.14 | 0.15 | 1.88 |
| | 21:00 | 0.26 | 0.15 | 0.91 |
| July 31 | 10:10 | 0.26 | 0.14 | 0.26 |
| | 14:20 | 0.17 | 0.17 | 1.11 |
| | 21:15 | 0.13 | 0.10 | 0.60 |
| August 1 | 10:10 | .......... | 0.21 | 0.24 |
| | 14:00 | .......... | 0.21 | 0.71 |
| | 21:10 | .......... | 0.14 | 0.41 |
| August 2 | 10:15 | .......... | 0.17 | 0.24 |
| | 14:15 | .......... | 0.16 | 1.09 |
| | 22:50 | .......... | 0.12 | 0.53 |
| August 3 | 10:10 | .......... | 0.15 | 0.34 |
| | 14:00 | .......... | 0.20 | 1.50 |

foliar transpiring for 24 consecutive hourly periods, the leaves selected here were closer together, and considering the relation

which is present between the leaves it would be expected that the variation would not be as great.

The data given in table VI show slowly decreasing values; however, the decrease is not marked. The highest foliar transpiring power for $Ib_1$ is 0.35, while the lowest is 0.10. The highest point as here set forth occurs on the 21st hour on July 26, while on the following day the index at the same time is 0.34. After that there is a slight fall, although this is not true for all the readings, for on July 30 the index is 0.31. Even at the time of wilting, the index at the morning hour is 0.26. From July 29 to July 31 the maximum values are approximately the same. This is also true of the minimum values. The last reading for the $Ib_1$ series occurs on July 31 and gives an index of 0.13.

For leaf $Ib_2$ the values are strikingly similar to those of the leaf situated just below it upon the stem. The highest transpiring power index for the entire time is only 0.28, and occurs at 9:35, July 26; while the minimum value 0.10 occurs on the 14th hour of July 29 and on the 21st hour of July 31. The data of table VI, represented graphically in fig. 5, show a gradual dropping off of the day maximum values from July 26 to July 30. From July 30 to August 3, with the exception of August 1, the graph of wilting is practically a straight line. On August 3 there is a marked increase, considering that the entire period has given a low index throughout (from 0.15 to 0.20, or an increase of 33.3 per cent). Usually during the march of foliar transpiring power a drop is registered at the 14th or 15th hour. On July 27 there is an increase of the index from 0.13 to 0.18 (38.46 per cent) and on July 31 from 0.14 to 0.17 (21.43 per cent). On account of the comparatively small deviation between the maximum and minimum values throughout, the increase in the transpiring power of one-third on August 3 becomes more significant than the graph shows (fig. 5).

The ratio between the day indices and night indices is presented as before, the readings of the 9th and 21st hours being used. On July 24 the morning reading is 0.17; on the following days the average foliar indices of transpiring power for leaf $Ib_1$ are 0.12, 0.12, 0.10, 0.22, 0.25, 0.31, 0.26. The corresponding night values are 0.18, 0.19, 0.35, 0.34, 0.12, 0.14, 0.26, 0.13. The corresponding

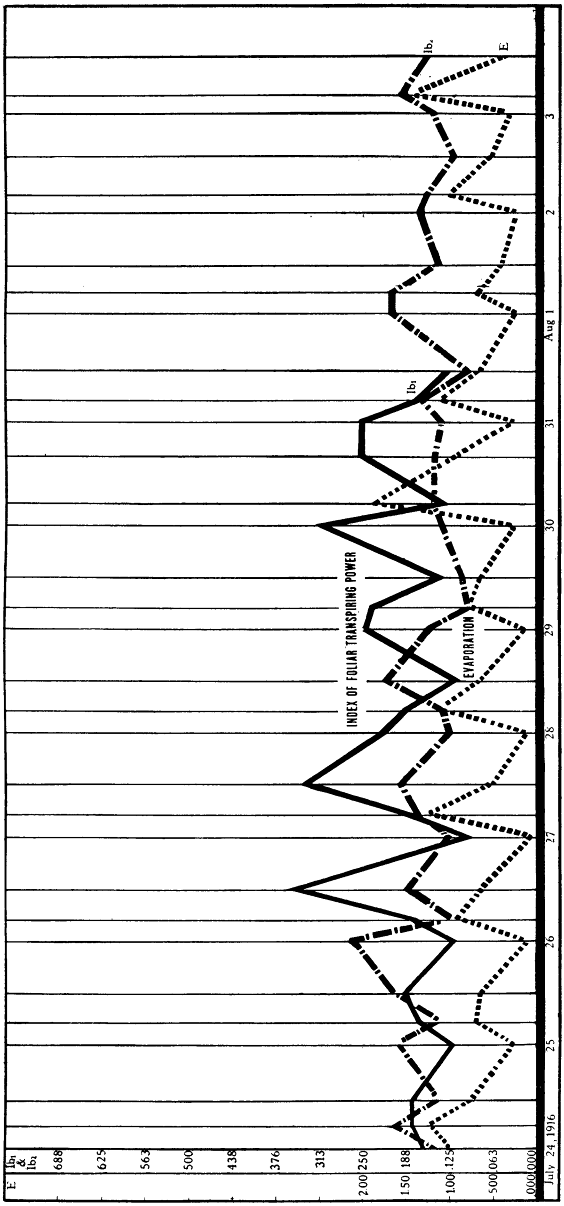
INDEX OF FOLIAR TRANSPIRING POWER
EVAPORATION
Ib1
Ib2
E
July 24, 1916
25
26
27
28
29
30
31
Aug 1
2
3
E
Ib1 & Ib2
.000 .000
.500 .063
1.00 .125
1.50 .188
2.00 .250
313
376
438
500
563
625
688

FIG. 5

ratios between the day and night readings are respectively 0.95, 0.63, 0.34, 1.83, 1.79, 1.19, 2.00. The ratio between the index of foliar transpiring power for the 9th and 21st hours on July 21–22 is 1.57. The ratio between the day maximum and the night minimum at that time is 2.11.

Taking into consideration that the minimum for I$b_1$ during the march of foliar transpiring power on July 21–22 is 0.49, the maximum values during the march of wilting are extremely low from the initial to the final point of wilting. On account of the drop in the maximum and the constant retentive character of the minimum, the index here is larger than recorded previously. The leaf was completely wilted on July 31.

The day values for I$b_2$ taken at the same time as before are 0.15, 0.20, 0.28, 0.13, 0.16, 0.14, 0.14, 0.21, 0.17, 0.15; while the corresponding night values are 0.14, 0.21, 0.19, 0.20, 0.22, 0.11, 0.15, 0.10, 0.14, 0.12. The ratios between these two sets are, in order of their occurrence, 1.07, 0.95, 1.45, 0.65, 0.59, 1.45, 0.93, 1.40, 1.50, 1.42. The ratio between the readings for the 9th hour and the readings of the 21st hour on July 21–22 for *Helianthus* leaf I$b_2$ is 0.98:0.51, or 1.92. The ratio between the maximum and the minimum is 2.23. In none of these cases can the proportion be regarded as normal. This plant from the beginning is evidently in a partially wilted state.

In comparing the march of foliar transpiring power during the process of wilting for the two series I*a* and I*b*, there would naturally be some variation. The wilting of series I*a* extends over a longer period (to August 7), while that of I*b* reaches its permanent wilting point on August 3. In both cases the older leaf wilts long before the younger leaf. However, leaf I*a* has a greater range of foliar transpiring power. Leaf I$a_1$ wilts before I$a_2$; likewise I$b_1$ before I$b_2$.

The ratio between the morning and the night readings of each day gives in the majority of cases a value that is less than the normal. For I*a* all the results are either near 1.00 or below it except for the first. As the maximum value is above that of the usual minimum the result cannot be anything but normal. With I*a* the ratio on July 31 is extremely high, probably being due to the

extremely high evaporation. Why there should be such a decrease at the 21st hour is not known. The first ratio 1.74 is approximately equal to the normal. The day reading is 0.68. The ratio on August 5 is 1.54, but the 9th hour reading gives a value that is much lower than the usual minimum. With a slight decrease in the minimum, the ratio between the two becomes greater than before. From these data on the basis of the ratio between day and night foliar transpiring power values it is evident that, if the ratio is to be used during the process of wilting, it can only be applicable when the maximum is greater than the usual minimum. Throughout the series of both I*a* and I*b* the ratio does not deviate very far from unity, but in the formation of the ratio there is an evidently greater corresponding decrease in the day value as compared with the night reading. In both cases the extent of daily fluctuation for the younger leaves is very small after the first day.

The rate of evaporation throughout fluctuated considerably, but is unusually high for the climate of Chicago. There is nevertheless no close agreement between evaporation and foliar transpiring power during the march of wilting. Plants similar to the ones used in the experiment were treated like I*a* and I*b* and were placed in a moist chamber at their respective times of wilting. They behaved in a similar manner and failed to recover in the allotted time. Although the plants were watered at the same time with approximately the same amount of water, figs. 5 and 6 show indirectly that there was much difference in the soil moisture content. The plant designated as I*b* was larger than I*a*, and would be expected to wilt first. This observation is borne out in the experiment. It is also evident from an examination of the two graphs that the soil of I*b* was drier at the beginning than that of I*a*, as the indices of foliar transpiring power are much smaller.

## STOMATAL DIFFUSION

The index of foliar transpiring power in its very definition is associated with that of vapor tension. The decrease in the index of foliar transpiring power such as is present at night during the daily march represents a great force. A solution may also carry with it just as great a force. LIVINGSTON (**27**), com-

menting upon FITTING'S (19) work upon the osmotic pressure present in desert plants, makes the statement that with the lowering of the vapor tension 10 per cent there is represented a pressure of 100 atmospheres. In an examination of the graph in table I there is a reduction in the index from 0.92 to 0.19 during the process of wilting. This therefore represents an approximate pressure of 800 atmospheres. For plant *B* there would be an approximate pressure of 700 atmospheres. Table V and fig. 4 give leaf I$a_1$ as being able to withstand a pressure of 666 atmospheres and leaf I$a_2$ 860 atmospheres. Leaf I$b_1$, with an index 0.10, suggests a pressure as high as 900 atmospheres. At that time the margin of the leaf was sufficiently dry so that the clip could not be used without causing injury. This status becomes all the more pertinent when it is compared with the data submitted by SHULL (41), where the force present in air dry seed (*Xanthium*) is equivalent to 1000 atmospheres.

During the daily march of foliar transpiring power there is usually considerable variation (figs. 2, 3), even when a plant is supplied with an optimum amount of water. The sudden rise in the foliar transpiring power immediately after sunrise, as set forth by BAKKE and LIVINGSTON, gives credence to the view that the stomata open quickly at this time. In using the porometer and standardized cobalt paper squares simultaneously, TRELEASE and LIVINGSTON (42) find that during the daily march there is considerable agreement between the porometer readings and the readings of the foliar transpiring power by the method of standardized cobalt chloride paper. From the results obtained in their investigation they concluded that the porometer gives readings which show the extent of stomatal diffusion.

DARWIN (12, 13), using the horn hygroscope and the temperature method, has shown that during wilting there is a temporary opening of the stomata. DARWIN and PERTZ (14), using the porometer, have demonstrated that a similar condition is present during wilting. LAIDLOW and KNIGHT (26) in their work upon stomatal behavior during wilting, where they employ a recording porometer, have confirmed the results of DARWIN and PERTZ, in that the stomata open temporarily during wilting. For *Phaseolus*

*vulgaris* the maximum diffusion occurred about 5 minutes after the leaf was severed from the stem, while in the case of the thick leaf of *Prunus Laurocerasus* nearly 20 minutes elapsed before the maximum stomatal opening was reached. KAMERLING (23) found that when *Rhipsalis cassytha* had lost 1 to 4 per cent of its normal water supply, the amount of transpiration per unit time increased, and later when the loss in weight had reached a certain point, varying from 6 to 10 per cent, the transpiration again diminished. KAMERLING is of the opinion that the increase in transpiration is due to the opening of the stomata. LLOYD (31), on the other hand, failed to find this temporary opening.

The evidences at hand support the conclusion that the stomata open for a short time during wilting. The time is short, however, and there is no evidence that the stomata ordinarily open up during the early stages of wilting and continue to be open until the plant has attained its permanent wilting point. This point is important in connection with argument presented for the break in the water columns.

In order to prove that the stomata open only during the early stages of wilting, the porometer as modified and used by KNIGHT (24) was resorted to. The plant was attached to the aspirator and allowed to remain until the leaves were partially wilted. Tests were made upon plants grown in the greenhouse and later transferred to the laboratory and plants which had been grown continuously in the greenhouse. The plants in the laboratory were kept for 5 days before experimentation was begun. The tests of this series were begun on November 28, 1917, and continued until December 3, 1917; readings were made at three different times of the day. This conforms with the plan adopted in making the readings of the foliar transpiring power. Evaporation was recorded by means of a standardized cylindrical form of atmometer of the Livingston type. The data are given in table VII.

In an examination of the data presented in table VII, readings were not taken until the 16th hour on November 29, 3 days after all watering had ceased. The time elapsing between two successive bubbles, as ascertained by means of a stop watch, was found to be 160 seconds. At the 11th hour it took 140 seconds, while

on December 1 at 10:30 it took 246 seconds. From that time until December 3 there was not much variation either at night or during the day.

TABLE VII

POROMOTER READINGS DURING PROGRESS OF WILTING OF A *Helianthus annuus* PLANT GROWING IN LABORATORY

| Time of observation | | | Rate of evaporation from standardized atmometer, cc. per hour | Rate of flow, time interval in seconds between successive bubbles |
|---|---|---|---|---|
| November | 27 | 16:00.... | .............. | .............. |
| | 28 | 8:00.... | .............. | .............. |
| | | 15:30.... | 1.45 | .............. |
| | 29 | 16:00.... | 0.72 | 160 |
| | 30 | 11:00.... | 1.12 | 140 |
| | | 14:30.... | 0.79 | 150 |
| | | 20:00.... | 1.34 | 146 |
| December | 1 | 10:30.... | 0.97 | 246 |
| | | 14:30.... | 1.11 | 266 |
| | | 20:00.... | 0.54 | 259 |
| | 2 | 10:30.... | 1.79 | 276 |
| | | 14:30.... | 1.71 | 260 |
| | | 20:00.... | 1.41 | 262 |
| | 3 | 10:30.... | 1.70 | 269 |

The data of the series grown continually in the greenhouse, where the evaporation was very low, are given in table VIII.

These results, which were obtained at regular intervals on 5 successive days (November 29 to December 3, 1917), do not show any marked differences. Considering the experimental error which would be present, there is not sufficient difference in any one case to indicate that stomatal movement was present. The plants used in this series were not watered for 3 days before the beginning of the experiment.

The stomatal diffusion as measured by the porometer was also determined for plants which were grown for the same period, but were not subjected to any extended period of wilting. The general average for the stomatal diffusion as represented by the time interval between successive bubbles of the air intake tube of a porometer was found to be 105 seconds. No attempt was

made to ascertain whether or not the stomata were partially closed or whether there was an increased opening after a period of 2 hours, as has been shown for certain plants by ILJIN (**20**). At any rate, the time interval in the case of intensely wilted *Helianthus* plants is much smaller. Even if the stomata should be partially

TABLE VIII

POROMETER READINGS TAKEN OF A WILTING *Helianthus* PLANT GROWING WHERE EVAPORATING POWER OF AIR IS LOW

| Time of observation | Rate of evaporation from standardized atmometer, cc. per hour | Rate of flow, time interval in seconds between successive bubbles |
|---|---|---|
| December 11 16:00 | .............. | .............. |
| 12 13:00 | 0.35 | .............. |
| 12 16:30 | 0.23 | .............. |
| 13 10:30 | 0.34 | .............. |
| 13 14:30 | 0.65 | .............. |
| 13 20:00 | 0.45 | .............. |
| 14 10:30 | 0.37 | 357 |
| 14 14:30 | 0.60 | 360 |
| 14 20:00 | 0.34 | 352 |
| 15 10:30 | 0.30 | 318 |
| 15 14:00 | 0.36 | 309 |
| 15 20:00 | 0.40 | 335 |
| 16 10:30 | 0.43 | 357 |
| 16 14:30 | 0.43 | 348 |
| 16 20:00 | 0.49 | 343 |
| 17 10:30 | 0.40 | 341 |
| 17 14:30 | 0.44 | 365 |
| 17 20:00 | 0.37 | 343 |
| 18 10:30 | 0.34 | 398 |
| 18 14:30 | 0.44 | 389 |
| 18 20:30 | 0.39 | 360 |

closed, the results obtained from tables VII and VIII show that during the march of wilting, where the plant acquires its permanent wilting point, the stomatal opening does not enter in to affect the diffusion or transpirational water loss. This statement is in agreement with that of DARWIN, that when the transpiration is high and the supply water insufficient the lack of water is a more important factor than stomatal changes. It would be extremely advantageous, however, to have the stomatal movement question

settled. Regarding the stomatal diffusion as a minor factor during intense wilting, the problem resolves itself to the point where the resistance to the passage is considered. From the data given in this paper and in a previous publication the resistance is exceedingly great. This will give further information, therefore, upon the strength of the evaporating force and that of cohesion.

## Discussion

In comparing the results obtained during the summer of 1915 with those of 1916, considerable additional evidence is set forth which substantiates the argument advanced by BAKKE that wilting occurs at a definite point and is readily determined by the use of standardized hygrometric paper. In the series of 1915 the average of 3 leaves were used in plant I*a* and 2 leaves for plant I*b*. No effort was made during the 1915 season to obtain the difference in the time of wilting for leaves of different ages. The difference, however, was probably very slight, as the evaporation was exceedingly low. At no time during the entire run was the evaporation as high as 0.7 cc. per hour, and usually it was below 0.5 cc. per hour. The temperature of the greenhouse was seldom over 28° C.

In contrast, the evaporation during the season of 1916 was high and during the time the experiments were being performed was exceedingly uniform. It may be added that during the progress of the experiment no rain fell. It would then have been preferable to have run the experiments outside, but in the climate of Chicago it is rather difficult to obtain such a continued period of clear weather. The usual feature will then be a low evaporation at night, a higher one during the forenoon, and the maximum at the 14th hour. The high evaporation rate on July 31 is not explainable. It may be well to remark, however, that on July 30 the temperature in the greenhouse was 41.2° C. and at the first hour of July 31 it was 27° C., almost the maximum of the previous year.

It is again brought out that for the 1915 and 1916 series a point is reached where the foliar transpiring power shows very little fluctuation. In the cases presented, this point can be represented graphically by a line that is almost straight. The ratio values are not far above unity in the majority of cases, and sometimes are

even lower. It is noted also that the time element of this period varies greatly in the two seasons. In 1915 it is comparatively short, while for both series in 1916 it is extended over a considerable period. It has been proved by the work of SHREVE (34) that plants grown under different environment not only have different anatomical characters but also have a different rate of transpiration.

On the basis therefore of a possible change as a result of environment, it can safely be asserted that this is the reason for the short span in 1915 and the long one in 1916. Why or how the plant establishes such an apparent equilibrium cannot be stated. This equilibrium represents the greatest force or tension which can be applied before a plant assumes the condition of permanent wilting. A plant such as *Atriplex* will necessarily have an extended period when this equilibrium is maintained. The exact wilting will be when there is a serious rupture in the water columns.

If this interpretation is correct, the 1915 and 1916 series should exhibit a difference in the foliar transpiring power values during the so-called equilibrium stage. It would be expected that the 1915 series would have a higher minimum than the 1916 series. This is evident, for in 1915 the lowest point reached at any time is never below 0.15, while for the 1916 series it is as low as 0.09 in one case and 0.10 in the other. There would thus seem to be a direct relation between the time of the equilibrium, the lowest point in the index of foliar transpiring power, and the evaporating power of the environment. The point at which wilting occurs is definitely marked out. This point appears graphically to better advantage for the plants of 1915 than for those of 1916; but the plants of 1915 were larger and were grown in smaller containers than those of the following year. For the series of 1915 the permanent wilting occurs on August 21, while for series I*a* (1916) the wilting occurs on August 7, and for series I*b* of the same year the wilting occurs on August 4.

In this study the same conception of wilting is advanced as before. The present study is really more or less of an elaboration of the former. It is assumed here that DIXON'S (**16, 17, 18**) con-

ception of continuous water columns is in force. When the force of evaporation becomes sufficient to cause a serious rupture of these water columns, then the plant wilts. Just to what extent a serious rupture can be regarded cannot be stated, but it must be greater than the force of cohesion which holds the water particles together.

The extent of this cohesion force has been sufficiently presented and advanced by DIXON (**16, 17, 18**), RENNER (**34, 35, 36**), URSPRUNG (**43, 44, 45, 46, 47**), and others (**21, 32**), and although the conclusions have been criticized by JOST (**22**), nevertheless they are substantiated. It is not the province of this article to enter into a critical discussion of these various papers. The approximate point of permanent wilting is readily ascertained from the beginning by taking a series of readings of the foliar transpiring power of the plant in question. Care should be taken to obtain in the series the maximum and minimum. Although there is not any hard and fast relation between the maximum and the minimum, when the moisture in a soil has been reduced to the point where the maximum is below the normal minimum, at a time of the normal maximum, then the water content of that soil has attained what the writer designates as the critical content. From this point it is simply a question of time when the columns break. This then becomes a relatively simple matter.

The readings giving the indices of foliar transpiring power taken at hourly intervals present a graph that is similar to graphs set forth previously. The maximum occurs at a time previous to the highest evaporation; the minimum generally occurs somewhere between the 18th hour and the 24th hour. There is a decided drop in the afternoon, which occurs at a time of day when evaporation is at its height or nearly so. There is a recovery that is also conspicuous. The cause for this resistance has been advanced by SHREVE (**40**) as being due to the imbibitional forces of the cell wall and of the colloids of the protoplasm. Although this feature has been noticed wherever the march of foliar transpiring power has been obtained, no one as yet has set forth any evidence as to the length of time necessary for recovery to take place. It is apparent that the recovery has been complete before the time of the

beginning of the next reading, which in this case is the next hour. A record of the foliar transpiring power at hourly intervals at Chicago gives results that are similar to those obtained for plants of the same species in southern Arizona.

The series of 1916 show conclusively that the older leaves are the first to wilt. In an examination of series I*a* the older set of leaves is almost completely dry at the time of the permanent wilting of the plant. On July 29 the edges of the leaf are dry, but at the same time there is a different form of response in the younger leaves, in that the apparent recovery occasioned at the time of permanent wilting does not present itself. The same situation is true for the series I*b*, where the older leaves wilt on July 31. That the older leaves are the first to wilt has previously been determined by a number of investigations (**15**, **33**). BAKKE and LIVINGSTON have presented evidence that there is considerable variation in the index of foliar transpiring power of young and old leaves. The fact that the younger leaves wilt later than the older leaves is not necessarily connected with the environment. This is true whether the evaporation is low or whether it is high. The production of the absciss-layer may at least be indirectly formed as a result. PRINGSHEIN (**33**) previously has shown that young leaves retain their freshness for a longer time than older ones. This he ascribes to a greater osmotic pressure. During the march of wilting it is also noticed that the foliar transpiring power index of the older leaves is always higher, at least than that of the leaves of the tip. The older leaves then give a higher foliar transpiring power throughout.

There is also in evidence during the march of wilting not only a low index of foliar transpiring power, but also a gradual increase of the force in opposition to the passage of water. When for a short time there is an evident break or a serious rupture, there is a decrease in the resistance, but an equilibrium with the atmosphere is soon reached. The assumption that there is a temporary opening of the stomata may be made at this point. Employing the porometer upon *Helianthus* plants placed in an environment of high evaporating power and one of low evaporating power, the author failed to find that the stomata are concerned.

## Summary

1. The transpiring power of plants as determined by standardized hygrometric paper gives an accurate knowledge of the internal water relations of a plant. The exact wilting point as determined by this method occurs when there is a serious rupture in the water columns.

2. During the daily march of foliar transpiring power obtained by making consecutive hourly readings for 24 hours, the maximum is attained at a time previous to the greatest evaporation. During the time of approximate maximum evaporation there is a marked fall in the foliar transpiring power index, followed shortly by a rise. The ratio between the maximum and the minimum is more or less definite, but not sufficiently so for the formation of any law. When the ratio is reduced to the point where it is in the neighborhood of unity, the plant is in a state of intense incipient drying. When the maximum value does not exceed the usual minimum, the plant is in a soil environment which is critical from the point of water supply, or almost at its wilting coefficient. It is then merely a question of time before the plant wilts.

3. Evaporation plays an important part in the experiment upon transpiration. A high evaporation gives an increased transpiring power value, but during the process of wilting the index of foliar transpiring power comes to be independent of evaporation.

4. During the process of the march of wilting an equilibrium point is reached where the indices of foliar transpiring power do not show much variation. It is suggested that the duration of the equilibrium gives a measure of the comparative drought resistance of different plants. *Helianthus* grown in 1915 during a rainy season is different from *Helianthus* grown during 1916, when the season was unusually dry. The equilibrium period of 1915 was much shorter than for 1916.

5. There is a decided difference in the time at which permanent wilting occurs in old and young leaves. The older leaves will wilt long before the younger ones. The time interval varies according to age.

6. Stomatal movements or changes are not important factors when the plant is in an intense state of wilting.

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